

Commentary

What does an insect see?

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Summary

The compound eye of the bee is an array of photoreceptors, each at an angle to the next, and therefore it catches an image of the outside world just as does the human eye, except that the image is not inverted. Eye structure, however, tells us little about what the bee actually abstracts from the panorama. Moreover, it is not sufficient to observe that bees recognise patterns, because they may be responding to only small parts of them. The only way we can tell what the bee actually detects is to train bees to come to simple patterns or distinguish between two patterns and then present the trained bees with test patterns to see what they have learned. After much training and numerous tests, it was possible to identify the parameters in the patterns that the bees detected and remembered, to study the responses of the trained bees to unfamiliar patterns and to infer the steps in the visual processing mechanism. We now have a simple mechanistic explanation for many observations that for almost a century have been explained by analogy with cognitive behaviour of higher animals. A re-assessment of the capabilities of the bee is required.

Below the photoreceptors, the next components of the model mechanism are small feature detectors that are one, two or three ommatidia wide that respond to light intensity, direction of passing edges or orientation of edges displayed by parameters in the pattern. At the next stage, responses of the feature detectors for area and edges are summed in various ways in each local region of the eye to form several types of local internal feature totals, here called cues. The cues are the units of visual memory in the bee. At the next stage, summation implies that there is one of each type in each local eye region and that local details of the pattern are lost. Each type of cue has its own identity, a scalar quantity and a position. The coincidence of the cues in each local region of the eye is remembered as a retinotopic label for a landmark. Bees learn landmark labels at large angles to each other and use them to identify a place and find the reward. The receptors, feature detectors, cues and coincidences of labels for landmarks at different angles, correspond to a few letters, words and sentences and a summary description for a place. Shapes, objects and cognitive appraisal of the image have no place in bee vision.

Several factors prevented the advance in understanding until recently. Firstly, until the mid-century, so little was known that no mechanisms were proposed. At that time it was thought that the mechanism of the visual processing could be inferred intuitively from a successful training alone or from quantitative observations of the percentage of correct choices after manipulation of the patterns displayed. The components were unknown and there were too many unidentified channels of causation in parallel (too many cues learned at the same time) for this method to succeed. Secondly, for 100 years, the criterion of success of the bees was their landing at or near the reward hole in the centre of the pattern. At the moment of choice, therefore, the angle subtended by the pattern at the eye of the bees was very large, 100–130 deg., with the result that a large part of the eye learned a number of cues and several labels on the target. As a result, in critical tests the bees would not respond but just went away, so that the components of the system could not be identified. Much effort was therefore wasted. These problems were resolved when the size of the target was reduced to about the size of one or two fields of the cues and landmark labels, 40–45 deg., and the trained bees were tested to see whether they could or could not recognise the test targets.

Key words: insect, bee, vision, cues.

Introduction

Little can be said about most insects but the honeybee is a special case because bees can be trained. Early researchers in the field trained bees with a number of patterns presented together, and the bees learned to land on the pattern that rewarded them with odourless sugar solution. The ability of the bees to recognise was related to a few parameters displayed in the patterns, namely the total length of edges in the pattern, the area and the colour, as if they had feature detectors for edges and also for brightness of areas. The bees also detected certain properties of the whole pattern, namely whether it was circular or had radial spokes or sectors and whether it was smooth or highly disrupted (Hertz, 1933). In very large simple patterns presented vertically and subtending >100 deg.,

the scores for the test patterns were related to the maximum overlap of the test area with the area of the training pattern (Wehner, 1969). Probably this strategy could not fail, whatever the mechanism. Later it was found that the bees learned the positions of areas of black in the periphery of the rewarded pattern and just below the reward hole (Horridge, 1996b). Towards the end of the century, individually marked bees learned to fly into an experimental choice chamber and select one of two patterns displayed vertically on the back walls (Fig. 1). It was fortunate that the patterns displayed on the targets subtended 40–50 deg. at the eye of the bee at the moment of choice and only one or two local regions of the eye were involved, so that the number of available cues was restricted and the mechanism could be analysed. At the centre of each pattern was

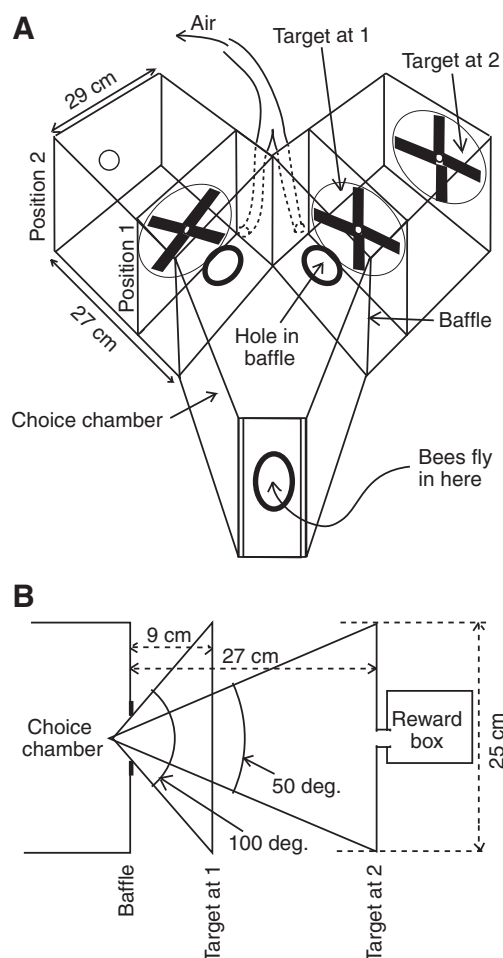


Fig. 1. (A) The apparatus for training bees with the target at a controlled range from the bees' decision point. The bees fly in the front, choose between the two targets and enter the hole in one of the transparent baffles. The targets, with the reward box behind one, are interchanged every 5 min. (B) Plan view of the angles subtended by the targets at two different positions 1 and 2 (Horridge, 2006b).

a hole but only one of these holes led to a small chamber behind it, where the bees found the reward. The two patterns (and the reward) changed sides every 5 min, forcing the bees look at them, rather than simply choose the rewarded side. There is no point in training bees and then not testing them to see what they learned, as frequently happened in the past. So, for the first time, the trained bees were given large numbers of tests in great variety. To prevent the bees learning them in the tests, different test patterns were intercalated and only one test was allowed between continued training periods.

Training and testing in the past two decades has revealed many more details of the bee visual system, so that a mechanistic model of the interactions between the input panorama and the recognition behaviour can now be presented. First, the three successive components of the visual processing will be described; these are the feature detectors, the cues and the landmark labels.

The feature detectors were isolated by using resolution tests, with modulation in displays of fine gratings, with orientation detected in rows of separate spots, squares, steps or the shortest resolvable edges and with areas of colour or black. The cues were inferred

from the numerous training experiments in which the bees could or could not learn to discriminate, and from tests of the trained bees with a wide variety of carefully designed test patterns displaying the known parameters. Then the order of preferences for the cues was found in tests with straight choices. Finally, it was realised that a single pattern was equivalent to a label on a landmark. Over some years, a comprehensive theory of the visual processing was assembled by persistently training bees and testing them (Horridge, 2006a).

The feature detectors

In each ommatidium of the compound eye, bees have three colour types of ordinary photoreceptors, with their spectral sensitivity peaking in the UV, blue and green. All three main types of photoreceptors have graded responses to intensity, so that passing edges cause a modulation (i.e. a change) in their responses. The receptors feed into an array of second-order neurons in the lamina that pass mainly the modulated part of the signal. The modulated inputs feed into several arrays of feature detectors (Fig. 2) with balanced excitatory and inhibitory inputs that are so arranged that they detect contrast at edges but are insensitive to widespread changes in brightness.

The pure modulation detector

The angular size of the pure modulation detectors with no orientation component was measured in the following way. Bees were trained to discriminate between a horizontal and a vertical black grating or between a grating of any orientation and a grey paper of matched brightness. The minimum grating period that was resolved by the bees was 2 deg. (Srinivasan and Lehrer, 1988; Horridge, 2003e). Because this result is less than the width of the field of view of a receptor (2.5 deg.), the modulation detector at the resolution limit is a single receptor with an inhibitory surround, which detects passing edges or spots (Fig. 2B).

The limit was little more when the grating was coloured to remove contrast to the green receptors. The orientation detectors have input channels only from the green receptors (Giger and Srinivasan, 1996). Therefore, the difference between the gratings with no green contrast was detected, not by orientation detectors but by radially symmetrical modulation detectors that resolve a 2 deg. grating with an input from blue or green receptors. Some of the modulation is detected as heterochromatic flicker and indicates any passing edge, not just small spots.

Feature detectors for edge orientation

Each feature detector for edge orientation is symmetrical about an axis of orientation (Fig. 2C–E), as shown by the inability of the bee to distinguish which side of an edge is dark and which is light. Their input is the modulation of green receptor responses and therefore they are colour blind. They detect the local orientation of a sharp or fuzzy edge within their field (Horridge, 2000a). They act independently, so they do not signal the continuity of a long edge. To measure the minimum angular size of the orientation detectors, bees that had been trained to discriminate between orientations of edges at 45 deg. and 135 deg. were tested with a large number of short parallel edges that were each reduced in length, but keeping the same total length of edge, until the orientation was no longer resolved. Square steps in an edge serve just as well as short thin bars. The minimum length of edge for the resolution of orientation was 3 deg. (Horridge, 2003d). Because the orientation detectors are only three ommatidia long, they are limited to three possible orientations of their axes (Fig. 2C–E) and have poor resolution of

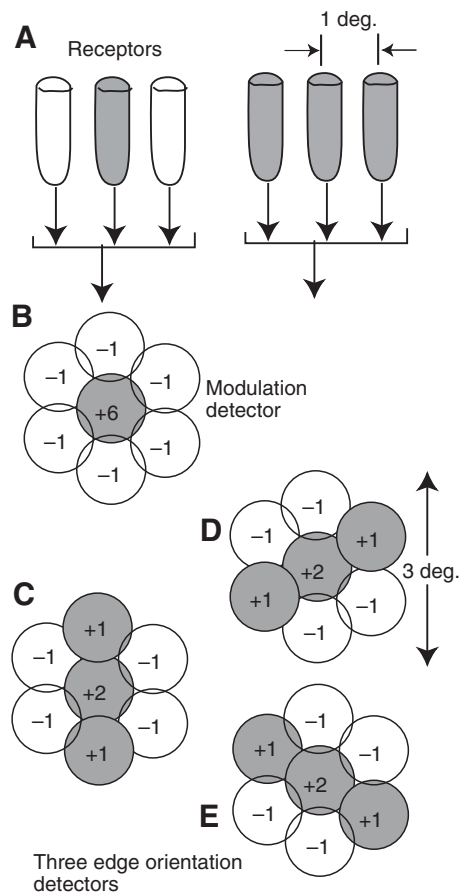


Fig. 2. From receptors to feature detectors. (A) The convergence of receptors on the four types of feature detectors for edges, all of which are insensitive to widespread intensity changes. (B) A radially symmetrical detector of modulation. (C–E) The detectors of modulation with bilateral symmetry (and therefore detectors of edge orientation) are green sensitive and colour blind. The numbers show the relative excitation (+) and inhibition (–) by light (Horridge, 2005).

differences in orientation. When the bees were trained on a black and white grating at 45 deg. *versus* the same grating at 135 deg., there was no difference in the modulation cue so the bees were obliged to use the less preferred difference in edge orientation for the discrimination, and the minimum period of the grating was 3 deg. (Horridge, 2003e).

The cues related to edges

Each cue is the sum (or count) of the number of responses of its own kind of feature detector within the local region of the eye (Fig. 3). Responses to parameters on one side of the target are processed separately from those on the other side, as if the bee fixates on the reward hole at the centre (Horridge, 1997b). The cues are in the bee and not in the pattern and must therefore be inferred from experiments. Because the cue is a sum, there is only one cue of each type in each local region of the eye. It is learned as a quantity in the range of positions where the parameters were displayed on the targets during the training (Horridge, 1999; Horridge, 2003a). The absence of a cue is itself a cue (Horridge, 2007). The bee detects, remembers and later uses the cues for recognition.

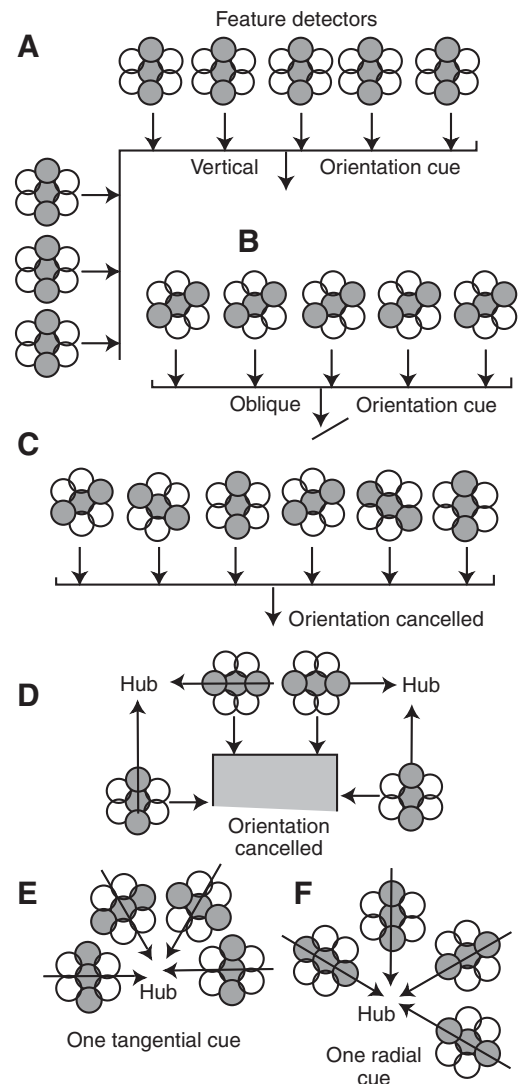


Fig. 3. Summation of feature detectors for edge orientations in various ways to form cues. Pattern is lost but cues emerge. (A) Detectors with vertical axes. (B) A line of detectors with oblique orientation. (C) Mixed orientations cancel but edge modulation and its position are retained. (D) The orientation cue is cancelled in the edges of a square but weak hubs are detected at the corners. (E, F) A tangential cue and a radial cue with their hubs.

This summation of many small parts of the pattern in various ways to form a few cues makes bee vision quite different from human vision or film. Firstly, in the most significant of the counter-intuitive effects the edges are summed separately from the areas of black or colour, and the totals make separate cues. Secondly, the edge detectors act independently so that the shapes of edges are lost. A long edge in a local region is indistinguishable from the same total of short edges parallel to it. Thirdly, edge detector responses are summed in such a way that equal lengths of components at right angles within the local region cancel the orientation (Fig. 3C,D). For example, a square cross subtending 40 deg. at the bee's choice point is not discriminated from the same cross rotated by 45 deg. (Srinivasan et al., 1994). Similarly, the orientation is destroyed when a bar is broken up into squares or cut into square steps that are separately resolved (Horridge, 2003c).

The greatest gap that can be spanned in a straight row of small squares is 3 deg., which is a measure of the maximum size of the feature detectors for edge orientation.

The feature detectors for edge orientation are small but summed within local areas that are up to 25 deg. across. The summation to form cues produces a summary of the local pattern within the region and greatly reduces the information content. There remains a measure of the average or predominant orientation of edges (Horridge, 2000a) and of the local edge modulation, i.e. a measure of the total length of edge (Hertz, 1933). The bees detect and learn the cues but the bees have no information about the distributions of the feature detector responses that were summed. There are also relatively few cues in a local region. Consequently, there are many pairs of different small patterns that the bees cannot distinguish. In tests, the trained bees accept familiar cues in unfamiliar patterns (with no unexpected cues added), because they know no better, having learned the cues for one pattern, not a vocabulary of cues for all patterns. This performance is called ‘generalisation’ in the bee literature but the actual patterns are of no interest to the bees (Horridge, 1996a; Horridge, 1997a; Horridge, 2009).

The responses of the edge detectors also collaborate together to detect the positions of hubs of radial or circular patterns in each local region (Fig. 3E,F). Possibly, there is only one of each of these cues at the front of the eye. The type of pattern, radial or tangential, and the position of the hub can be learned but again the local layout of the feature detector responses is lost in the summation (Horridge, 2006b).

Despite many searches, surprisingly few parameters and their corresponding cues have been discovered (Fig. 4). All of the cues are formed by a distributed mechanism of summation, not by preformed templates. There is an order of preference for learning the cues in the training situation, with modulation the most

preferred, then position of centre, area, a black spot, colour, radial edges, bilateral symmetry, average orientation and finally tangential or circular edges, which are avoided (Horridge, 2007). This is a small but apparently adequate variety for the life of a bee.

Most of the natural panorama exhibits a variety of orientations of edges with a strong modulation cue for bees but usually most orientations cancel out, so only the edge modulation and its position remain. Here and there, however, the bee encounters parallel edges, for example in grass, and occasionally the significant symmetry of a flower or spider’s web. The mechanism outlined shows that statistics of natural images, such as spatial frequency, are of little use for understanding bee vision before the feature detectors and cues have been described.

Cues related to areas

The components that detect areas of black, colour or bee white (which is near human green), appear to be the photoreceptors themselves. Their responses are separately totalled within the local areas on each side of the target, so that detail and shape are lost. Unlike human vision, the feature detectors and cues for an area are separate from those for its edges and are summed over eye regions of different sizes. This separation of areas and edges implies that the visual signals leading to memory are hard for humans to visualise but they can be easily computed in machine vision. Areas are detected as (number of receptors × brightness) (Wolf, 1935) with the position of their centre but no information about shape is encoded (Horridge, 2003b; Horridge, 2005; Horridge, 2009).

Bees discriminate between some small shapes by the cues for average edge orientation that are detected separately on the two sides (Horridge, 2006c; Horridge, 2009), not by the form of a closed boundary, which is lost in the distributed summations (Fig. 3). Patterns with different positions of blue, green and yellow areas are usually discriminated (von Frisch, 1914; Gould, 1985; Gould, 1990; Horridge, 2000b) but not all differently coloured areas are learned separately; blue being the preferred and sometimes the only colour position learned, even when it is on the unrewarded target (Horridge, 2006c; Horridge, 2007). One cannot infer that a pattern of colours is learned without testing each colour in a variety of places on the target.

The positions of the centres of two areas of black or colour can be remembered as cues but where they are close together (within a local region), the bees remember only their common centre and total area. Merging of the two areas diminishes as the spots move apart, from an angle subtending 5 deg., until at 15 deg. they are separate (Horridge, 2003b).

Labels for landmarks: place recognition

The group of cues that are detected at the same time by a local region of the eye form the label for a landmark (Fig. 5), irrespective whether there is a single or several actual landmarks in that part of the panorama (Horridge, 2006b; Horridge, 2007). The landmark label can be learned. All that matters is that the bees remember the coincidence of responses of cues in that local region of the eye. There is no evidence for, and much against, the permanent grouping of cues in memory. This kind of vision differs from human vision also because the angle subtended by the panorama is so large, and the bees are interested in the angles between landmark labels, not in the shapes of objects.

The feature detectors have a position, a quality or identity (for modulation, vertical edge orientation, etc) and a quantity of unity. The cues each have a position, a quality or identity (for modulation, average orientation, etc) and a quantity, which is a sum.

Feature	Weak	Strong
Modulation		
Position of black		
Area		
Radial		
Bilateral symmetry		
Orientation		
Tangential		

Fig. 4. The seven common parameters that approximate to cues, in order of preference in the learning situation. This illustration is only to assist the reader visualise the cues, which are actually in the form of excitation in a column of neurons within the bee. The position of the centre of a black area is learned preferentially near the reward hole or in the periphery of a large (>100 deg.) pattern.

Significantly, these are almost the properties of neurons. Similarly, the landmark labels each have a position, an association with a place and a coincidence of cues. The whole process from receptors through to feature detectors and then to cues and landmark labels (Fig. 5) is done region by region on the eye and therefore in coordinates related to the position of the head and body axis. For this reason, bees scan the scene in the horizontal direction as they fly, and orient their head and body to detect landmark labels that

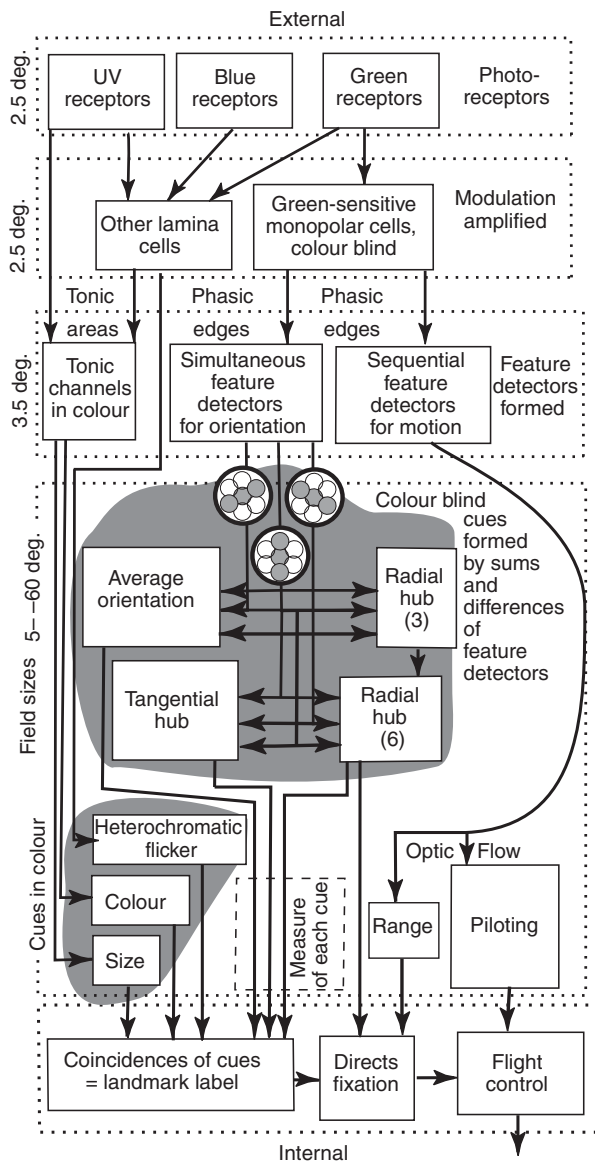


Fig. 5. A map of the formal interactions between the different processing channels to form a landmark label in a single local region of the eye. This diagram is a summary of the whole mechanism in a local region behind the eye. The receptors at the top feed through the lamina to feature detectors, the responses of which are summed to form cues. The coincidences of cues form a landmark label. One local region like this is therefore trained for one task, with insufficient information to distinguish all patterns. Approximate field sizes are shown on the left. Any resemblance to the bees' optic lobe is not accidental (Horridge, 2005). Bees discriminate between radial symmetry based on three parts and six parts, and also between each of these and the corresponding orthogonal radial pattern, so there are at least two types of radial hub.

bring them to the place of the reward. Learning the labels and recognition of a place must be done by 'operant' conditioning, which is part of 'active vision'.

The effect of pattern size

In the earliest experiments the criterion of success was the bee's landing on the target. It was thought that the bees learned the whole pattern because they recognised isolated circles and radial patterns, apparently as a whole, irrespective of the exact size and number of radial arms. The intuitive inference was that the bees learned the abstract idea of the shape, possibly in any orientation (Hertz, 1933).

This idea was eventually rejected by training bees with smaller patterns of controlled angular size <45 deg. (Fig. 1), so they learned only one or two landmark labels. The trained bees were presented with the training pattern *versus* quite a different pattern, which produced the same preferred cues and no unfamiliar cues. The trained bees showed equal preference for the new pattern and the one they were trained on, and their preferences were changed by the addition or removal of cues, showing that they were interested in the cues, not the patterns (Horridge, 2006a; Horridge, 2009).

As shown by the separate identification of the parameters on the two sides of the target, a small pattern that subtends 40 deg. or less in the Y-choice apparatus is usually divided between the two eyes if the bee is able to fixate on the reward hole in the centre (Horridge, 1996a; Horridge, 2006a; Horridge, 2006b; Horridge, 2009).

Very large patterns subtending >100 deg. are learned in a different way because they overlap several local eye regions and therefore the bees learn several labels and something about the configuration of the regional positions of all cues (Fig. 6C). Large patterns are discriminated for preference by differences in the positions of black or colour in their peripheral parts (Wehner, 1969; Horridge, 1996b). The same applies when the criterion of success is the landing of the bee on the target (Lehrer and Campan, 2006). It is difficult to test bees that have been trained on very large targets because they have learned several labels and perhaps many cues, so they just go away when presented with an unfamiliar test pattern. It was possible to analyse the feature

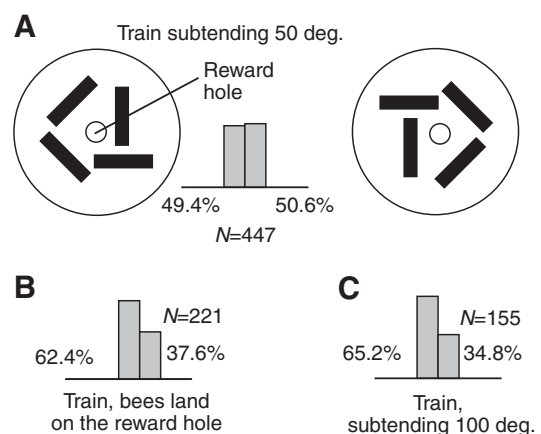


Fig. 6. The importance of controlling the angular subtense of the target. (A) At a subtense of 50 deg. or less, the bees cannot learn to distinguish between these two patterns that are obviously different to us. Neither the whole patterns nor the positions or orientations of individual bars are recognised in a target of this size. (B) The bees learn to discriminate these patterns when the criterion is their landing on the target or (C) when the target subtends 100 deg. or more in the apparatus in Fig. 1 (Horridge and Zhang, 1995).

detectors and cues only after the subtense of the target was reduced to 40–50 deg. Before the effect of target size on the recruitment of local regions was understood (Fig. 6), conflicting results were obtained with targets of different sizes and analysis was delayed for almost a century.

It is essential to study the effects of target size (Figs 1 and 6) to measure the size and resolution of the local regions. The ability of the bee to discriminate the shape of an object by the positions of peripheral edges and areas is governed by the angular size of the target as seen from the point of decision, because the size of the local eye regions appears to be fixed. The bee eye has a total angle of about 300 deg., which is probably divided into 10–20 local regions for the formation of cues (Fig. 7). This is more than sufficient for the discrimination of a pattern when the bee lands on it and discriminates the layout of patches of black (Lehrer and Campan, 2006) or recognises a familiar place by a few landmarks (Fry and Wehner, 2002).

Resolution in the processing hierarchy

Resolution at any level in the system depends on the angular subtense and shape of the field of the detector and on the separation between detectors, not the interommatidial angle (Horridge, 2005). At the level of coincidences of receptor responses that form feature detectors, we have a resolution of 2 deg. for modulation. On account of the lateral inhibition (Fig. 2B), this is better than for a single receptor. Honeybees can detect a small black spot that subtends an angle of 2–3 deg., orientation in a minimum length of edge that subtends an angle of 3 deg. and angle of orientation in a grating with a period of >3 deg. A bee's resolution of the angle of orientation of an edge on a vertical surface is poor because the feature detectors are independent and so short. With patterns subtending <40 deg., an orientation difference of 45 deg. is the limit for a single bar, 30 deg. for a parallel grating.

The size of the summation field that determines the resolution of cues is not the same for each cue. They are: modulation in

regions of 20 deg. across; residual edge orientation in regions of 15–20 deg. across; position of areas of black or colour, 12–16 deg.; and position of the centre, 5 deg. At the level where coincidences of cues form a landmark label, we have overlapping areas up to 45 deg. across, and a minimum separation of about 15–20 deg. between neighbouring landmarks. The three stages of processing have resolutions of ~2–3 deg., 15–20 deg. and 30–40 deg. (Horridge, 2005) but the resolution of the position of a landmark can be as small as 5 deg.

Design of the bee visual system

The extremely wide visual field of the insect compound eye detects approaching enemies and the direction of an open flight path. In the bee, the wide field has other functions. At every moment, bees remember their direction relative to the sun-compass and the direction of home. They also recognise places by landmarks detected at large angles on the eye (Collett et al., 2002). A landmark is not necessarily an isolated object, it can be parts of distributed branches, flowers or pebbles that display sufficient coincidences of cues to make a label in a local eye region.

The mechanism of discrimination is a very simple progressive summation and detection of coincidences in a hierarchy that is typical of sensory integration throughout the animal kingdom. At each stage in processing, there is a compromise between the resolution, which is better in small summation fields, and the sensitivity or the ability to find the target, which is better in large fields. In the bee, processing is designed for detection of the coarse configurational layout of the local combinations of cues in a 300 deg. visual field, which is nothing like human vision.

It will be noticed that nowhere are objects or patterns of any interest to the bee. No new detectors or cues are generated to match the elements in the panorama. Patterns with outlines were introduced to bees as oriented bars, spots, stars or triangles in the early days of bee training and persisted as experimental tools for a century. Bees appeared to distinguish between them but actually they detect only a combination of landmark labels to identify a place. Patterns and objects are for people: bees detect parameters and remember cues.

Where does learning occur?

The bees have no reason to remember the responses of the individual receptors or feature detectors and there is no evidence that they do. They behave as if they continually learn and unlearn the cues in a quantitative way, and each local region of the eye acts independently up to this stage. The cues in each local area form a landmark label (Fig. 5) probably where large field neurons converge towards the base of the optic lobe. The cues in a local region behave like a set of independent, preformed boxes that can be ticked, and when the same combination recurs, the landmark label is automatically recognised because each cue is recognised in its position. This process happens in each local area, then again in the eye as a whole (Fig. 7). At this stage, the bees remember several coarse retinotopic projections of labels that are quantitative summaries of places.

Generalisation of patterns

In all studies of bee vision, generalisation was defined as the acceptance of an unfamiliar pattern by trained bees in the place of the familiar training pattern. Also, last century it was found that bees could be trained with a variety of different squares or equilateral triangles that were presented simultaneously or in succession, called 'generalisation in the training' (Hertz, 1933;

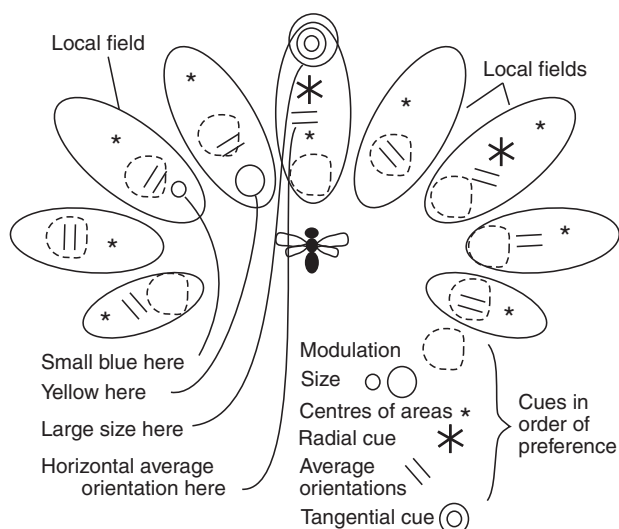


Fig. 7. A representation of the display in the panorama that is detected by the bee. Each oval subtending about 30 deg. represents a local region in the bee eye. Within each region no more than one cue of each kind is detected. The coincidences of cues that have been learned in several regions of the eye enable the bee to recognise a familiar place or a very large target with little error (Horridge, 2005).

Anderson, 1977). The trained bees could also recognise the familiar training pattern when it was presented at a different size. It was concluded that the bees learned an abstract feature that was common to the different targets. These abstract features turned out to be the usual local internal totals of feature detector responses (cues) that were detected in parallel.

When bees are trained in the Y-choice apparatus, patterns of constant size are interchanged every 5 min to make the bees look at them (Fig. 1). The bees learn to ignore local cues outside the pattern, which restricts their field of view as if they are wearing blinkers. In the experimental apparatus, each side of the pattern is approximately the size of the local eye region, and the bees tend to look at the reward hole in the centre, so that only one cue of each type, and therefore one label, is learned in each eye. The pattern becomes one or two landmarks that locate the reward. This is sufficient for the task in hand but is insufficient information to distinguish the training patterns from many other patterns that display the same cues.

The mechanism described accepts an unfamiliar pattern as long as the familiar cues are detected near the expected positions and no unexpected cue is added. In its responses to tests, a bee trained on a pattern subtending 40 deg. is similar to a cheap lock that is opened by several keys. A bee trained on a natural place with several landmarks resembles an expensive lock that is opened by only one key.

Generalisation in bee vision is therefore nothing to do with cognition or recognition of an abstract similarity or difference. It is a consequence of a training that was restricted to one task with a relatively small target that generates only one or two labels. Errors of recognition are less likely when the training pattern is very large, so that it extends over several eye regions (Fig. 6C; Fig. 7). Before making comparisons of generalisation in the vision of different animals, it is essential to understand thoroughly the mechanisms in each example.

Misleading terminology

Words and phrases borrowed from the cognitive sciences, such as 'perception of shape', 'similarity', 'triangularity' and 'recognition', supported anthropomorphic ideas about mysterious cognitive abilities of the bees. Even a pattern, a shape or a regular grating, however, are no more than places that display cues. Expectations are also disappointed when a remarkable performance of the bees is described in different words, terminology is borrowed from the behaviour of higher animals, then new powers are attributed to the bees and proclaimed in the title of the publication. To avoid unjustified conclusions, even a mild phrase such as 'discrimination of difference', when translated for the bee, becomes 'cue from one but not the other' or perhaps 'avoid unfamiliar parameter' but nothing more.

Every researcher on bee vision has fallen into the anthropomorphic trap. Even a plain description of bees learning to discriminate between two patterns can be taken to imply that they see the whole patterns (Gould, 1990). In examples where bees discriminated between two objects or faces, it was observed that the bees, after long training, distinguished them correctly (after poorly performing bees were disregarded) but, on no evidence at all, it was intuitively inferred that the whole pattern was remembered and 'generalised' (Dyer et al., 2005; Dyer and Vuong, 2008). With one training experiment, with huge targets, one cannot conclude anything about mechanisms, much less extrapolate to all insects. After all, Aristotle was aware that bees that nest in a hollow tree can distinguish their tree from the others.

It is impossible to show that the bees see the whole pattern, because in every case they may be detecting only a small part of it, as demonstrated by Hertz for the bee (Hertz, 1933) and Lashley for the rat (Lashley, 1938). However, it is easy to show that trained bees show equal preference for the original training pattern and different patterns that display the same cues and they respond to added cues. Therefore, they learned the cues, not the pattern. Training bees to discriminate two patterns or objects is an entirely artificial situation in which they adopt their usual strategy of locating and measuring cues to identify the place of the reward.

In the recent examples quoted above, the bees were allowed to examine closely the pictures of faces, so they subtended very large angles. Spots, dark patches or marks could have contributed to make more than one landmark label. The trained bees were not tested as to what they had actually learned. With patterns of comparable size at the moment of choice, when the criterion was also the landing on the pattern, the bees identified the positions of patches of black in widely separated positions on the periphery (Horridge, 1996b; Lehrer and Campan, 2006).

Problems of analysis

For the whole of the past century bee vision was a mystery. In particular, the kind of system involved was unknown. The components were not listed. There was no systematised way, no paradigm, to help find the crucial questions to ask. Usually the trained bees were given few different tests and even then more than one variable was changed at a time. It was not understood that bee vision is adapted to a mechanism of recognition of places that requires a 300 deg. not a 40 deg. field of view. Pattern subtense was not controlled, except in work by Wehner, sometimes not even mentioned. It was a major problem to discover what the bees actually detected. Work on other visual systems was of little help, because they were quite differently organised and usually even less well understood. The convictions of the experimenters about the cognitive abilities of the bees delayed progress. It was thought that bees actually see the world or some aspects of the panorama as a pattern of pixels, even if fuzzy. It was thought that bees recognised objects and used them as beacons. It was anti-intuitive to conclude that areas were disconnected from their edges and most of the pattern was the redundant part of the input.

The bees learned to come to patterns that were shuffled about, and the experimenters were convinced that the bees recognised and remembered the patterns. But bee vision is hopelessly counter-intuitive. The experimenters could not detect the cues: the bees could not detect the patterns. Any combination of contrasts could be a landmark for a bee. Hundreds of tests of trained bees were required before the actual cues were identified.

Finally, to rule out alternative explanations, it was shown that when trained bees were tested with the training pattern *versus* a different pattern that displayed the same cues, and no unexpected cues, they did not distinguish the pattern they were trained on. That experiment was repeated for all the kinds of patterns that had been used to train bees (Horridge, 1996a; Horridge, 2006a; Horridge, 2009).

Image processing is only half of the visual system

This analysis of the formal interactions of the inputs and cues in bee vision would be little more than elementary common sense in computer vision. There are three successive arrays laid out in the angular co-ordinates of the compound eye. The edge detectors (Fig. 2) resemble Canny edge detectors (used in computational

image recognition) and are only 3 deg. in size. Individually the positions of the feature detectors are not remembered. Each type of feature detector is summed to form one cue in each local eye region (Fig. 5). The coincidence of different cues that occur at the same time in a local region is the only retained information about that part of the image. The coincidence of landmark labels is recalled only for the recognition of a place (Fig. 7). There is little sign of neural control of field sizes.

The described mechanism is only half that required for practical use, however, because the visual processing is fixed in position in the eye, which is fixed on the head on the body. The bee scans in the horizontal plane while in flight, and the posture and movements are controlled by the vision itself. Learning is therefore operant, i.e. controlled by the animal's own movements, with instant feedback. The eye is useless without its control of its own moving platform. Understanding how eye movement is controlled is the next frontier.

Conclusion

The new results illuminate many themes. Firstly, most relevant to the recent literature, there has to be improved justification for intuitive inferences that go beyond a simple mechanistic explanation. Secondly, the feature detectors and cues can now be sought by electrophysiology. Thirdly, the mechanism illustrates how the information in a picture or panorama can be greatly reduced and yet reasonable recognition by a simple mechanism is preserved. Perhaps more interesting, the evolution of bee vision has reached the glass ceiling where no further processing can be done without moving to the next stage, which is the re-assembly of the pattern, which requires vast extra processing power. Also, the bee provides us with a blueprint for an artificial seeing system that has been evolved for the recognition of places on a large or small scale, with minimum components and weight that might be useful for machines with computer vision. The memory mechanism is not like wax that takes up any shape but is a set of independent, preformed boxes that can be ticked, and when the same combination recurs, the place is automatically recognised. Finally, this small self-contained topic, the training and testing of the vision of bees, illustrates the circuitous route and unpredictable nature of research, which is always waiting for new concepts and techniques.

Glossary

Active vision

Active vision is vision by scanning or with any active movement.

Cue

A *cue* is the sum or count of the responses of one kind of feature detector in a *local region* of the eye and is therefore inside the bee. The *cue* is derived from the parameters but the process of summation in the local region destroys the local layout of the pattern. Bees learn *retinotopic positions* of cues. Some cues are measured quantitatively. There is an order of preference for the known cues.

Feature detectors

The *feature detectors* behind the eye respond to the parameters. The *feature detectors* are the units of perception of modulation, edge orientation, black, white or colour. They are small, about three ommatidia across on the retina, and all respond independently in parallel. The responses of the different feature detectors are separately summed to form corresponding cues, and the bee remembers the totals and their positions, not the individual detector responses.

Field of view

The *field of view* of a filter or neuron is the region in space and time within which a signal is detected.

Fixed pattern

A *fixed pattern*, as opposed to a *shuffled* one, has the pattern fixed as seen from the choice point of the bee.

Generalised parameter

A *generalised parameter* is one that is recognised in a context other than in the training pattern. Originally it was merely in a different position on the target but later it was in a different pattern.

Image

The *image* is the pattern of excitation in the array of receptors in the retina.

Lamina

The *lamina* is the layer of neurons and synapses forming the first optic ganglion immediately below the photoreceptors.

Landmark

A *landmark* is recognised as the coincidence of several different cues in a local region of the eye.

Landmark label

The *landmark label* is the coincidence of cues in a local region of the eye, by which the bee recognises a landmark and its position.

Local region

A *local region* of the eye is the area of the field of view of a cue or landmark label.

Modulation

The *modulation* of a receptor is the change in the light intensity in the receptor and the consequent electrical signal. The motion of the eye over *contrasts* generates the modulation of the receptors. The *modulation* of a pattern is roughly equal to the total length of edges in it.

Ommatidium

An *ommatidium* is a unit of the retina, consisting of a transparent facet, optical path and a group of nine photoreceptors.

Operant conditioning

Operant conditioning is the term for learning as a result of one's own trial-and-error efforts and implies active vision.

Orientation

Orientation of an edge is usually the angle to the vertical in a vertical plane. Within the local region of the eye, orientation has a retinotopic position that bees can be trained to remember.

Parameters

The *parameters* are parts of the image outside the eye. A *parameter* is a scalar or vector measurement of some aspect of the pattern outside the eye, e.g. the area, total length of edge or averaged edge orientation.

Patterns

The *patterns* are displayed on the *targets* during training and tests.

Place

Place for bees is a geocentric term, like the place on a map; *position* and *direction* are usually retinotopic terms for the direction relative to the axes of the head. *Location* or *position* also refer to the position of a parameter on the target, a shift in position of a pattern or a shuffle of the locations of boxes, targets or bars during training and tests.

Point of choice

Point of choice is the place where the bee detects a cue and makes a choice by moving away or towards the reward or the next target.

Receptors

The *receptors* are the sensory nerve cells in the retina.

Unit of vision

A *unit of vision* is the smallest distinguishable element at that level.

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